

PAPER • OPEN ACCESS

Plant and soil microbial responses to irrigation retirement in semiarid cropping systems

To cite this article: Agustín Núñez *et al* 2022 *Environ. Res. Commun.* 4 035004

View the [article online](#) for updates and enhancements.

You may also like

- [Conceptualization of cultural sustainability for elderly Pondok Village \(EPV\)](#)
K Ismail, K Alauddin, Y Abdul Talib et al.
- [Efficient algorithm for locating and sizing series compensation devices in large power transmission grids: II. Solutions and applications](#)
Vladimir Frolov, Scott Backhaus and Misha Chertkov
- [Utility-specific projections of electricity sector greenhouse gas emissions: a committed emissions model-based case study of California through 2050](#)
Emily Grubert, Jennifer Stokes-Draut, Arpad Horvath et al.

Environmental Research Communications



PAPER

Plant and soil microbial responses to irrigation retirement in semiarid cropping systems

OPEN ACCESS

RECEIVED

22 December 2021

REVISED

17 February 2022

ACCEPTED FOR PUBLICATION

2 March 2022

PUBLISHED

17 March 2022

Original content from this work may be used under the terms of the [Creative Commons Attribution 4.0 licence](#).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.

Agustín Núñez^{1,2,3} , Ryan Ball¹ and Meagan Schipanski¹ ¹ Department of Soil and Crop Sciences, Colorado State University, 307 University Ave., Fort Collins, CO. 80523-1170, United States of America² Instituto Nacional de Investigación Agropecuaria (INIA), Estación Experimental INIA La Estanzuela, Ruta 50 km 11, Colonia 70000, Uruguay³ Permanent address: INIA La Estanzuela, Ruta 50 km 11, Colonia 70000, Uruguay.E-mail: anunez@inia.org.uy**Keywords:** dryland agriculture, soil moisture, crop productivity, root:shoot ratio, soil enzymes, PLFA analysisSupplementary material for this article is available [online](#)**Abstract**

Water scarcity limits irrigated agriculture, and there is an increasing frequency of situations where farmers must transition from irrigated to dryland cropping systems. This transition poses several challenges, and it is necessary to understand the changes in crop productivity and soil health for the design of viable cropping systems. Our objective was to compare the impact of irrigation retirement on crop production and soil microbial dynamics under the two major crops of the semiarid High Plains. In a formerly irrigated field, we installed a transition experiment that consisted of two irrigation managements, irrigated and non-irrigated (retired), under two cropping systems: continuous maize and continuous winter wheat. Lower soil moisture after irrigation retirement decreased plant biomass production in both crops, with a higher effect on maize (2 to 6-fold decrease) than on wheat (20% less aboveground biomass production). In both crops, irrigation retirement affected crop development in the order grain yield > aboveground biomass > belowground biomass. Soil microbial communities were less affected by irrigation retirement than the evaluated crops and changes were concentrated in the maize agroecosystem. After three seasons, the high decrease in maize productivity and soil moisture resulted in 50% less extracellular enzyme activity in the dryland treatment, but without consistent effects on microbial biomass or community composition assessed by phospholipid fatty acids. Winter wheat appears as a viable option not only to sustain crop production but also to minimize the negative impacts of irrigation retirement on soil health. However, root production was lower in wheat than in maize, which may affect the long-term evolution of soil organic carbon.

1. Introduction

Agriculture consumes 70% of global water withdrawals (FAO 2011). In some key agricultural areas of the world this consumption is unsustainable because it exceeds the local availability of water resources (Davis *et al* 2018). Moreover, the competition for water resources is growing as municipal and industrial demands increase and water availability decreases (FAO 2011). Thus, there is an increasing pressure to reduce agricultural water consumption. The Ogallala Aquifer Region (OAR) provides one example of this situation. The Ogallala Aquifer, one of the most important aquifers in the world, has a great influence on the production value of the High Plains of the United States (Hornbeck and Keskin 2014, García Suárez *et al* 2018). However, the rate of water withdrawals to support irrigated agriculture across many parts of the aquifer exceed recharge rates, leading to declining groundwater levels (Richey *et al* 2015, Smidt *et al* 2016). To extend the life of the Aquifer and to meet water requirements from other users, pumping rates for agriculture must decrease (Whittemore *et al* 2016), and

an increase in the transition from irrigated to dryland is expected in the region. This transition poses several challenges for the agricultural systems of the region as both crop productivity and soil health will be impacted.

Maize and winter wheat are the dominant crops in the central and northern parts of the Ogallala Aquifer Region (OAR). Maize is the predominant irrigated crop and most of the water for irrigation comes from the Ogallala Aquifer (Norwood 2000), while winter wheat is the dominant crop under dryland production (Hansen *et al* 2012, Rosenzweig and Schipanski 2019). During the last decade approximately 50% of the maize area was under irrigation in Colorado, Kansas, and Nebraska, while irrigated wheat represented less than 10% of the total winter wheat area (USDA-NASS 2017). In the same period, irrigation increased maize yields by 80%–160%, while winter wheat yields with irrigation were on average 60% more than under dryland (USDA-NASS 2017). Correspondingly, irrigated cropping systems had more crop residue production, which resulted in almost three times more soil C inputs than their dryland counterparts in farms of eastern Colorado and western Nebraska, the western and more water-limited portion of the northern OAR (Denef *et al* 2008). This difference in C inputs resulted in 27% more soil organic carbon (SOC) in irrigated cropping systems relative to dryland systems at 0–20 cm soil depth (Denef *et al* 2008). Thus, irrigated systems are more productive and have more SOC than their dryland counterparts.

Soil organic carbon plays a key role in supporting many of the agronomic functions provided by soils (Rawls *et al* 2003, Oldfield *et al* 2019, Wade *et al* 2020, Kane *et al* 2021) and is an important indicator of soil health (Cano *et al* 2018, Lehmann *et al* 2020). However, SOC changes slowly, and many years may be necessary to quantify its changes (Smith 2004, Bradford *et al* 2016). Soil microbial community composition and activity affect SOC formation, nutrient dynamics, and other important soil functions (Acosta-Martínez *et al* 2011, Kallenbach *et al* 2016, Fierer *et al* 2021) and respond to environmental changes faster than total SOC (Franzluebbers *et al* 1994, Ndiaye *et al* 2000, Acosta-Martínez *et al* 2011). Because of this, several measurements of microbial processes have been proposed as indicators of soil health that can indicate early changes in SOC and nutrient dynamics (Acosta-Martínez *et al* 2011, Cano *et al* 2018, Lehmann *et al* 2020, Fierer *et al* 2021). Among many options, the estimation of microbial biomass and community composition via phospholipid fatty acid analysis (PLFA), and enzyme activity are usually suggested as biological soil health indicators informative for many of the ecosystem services provided by soils (Cano *et al* 2018, Lehmann *et al* 2020). In the long-term, changes in litter inputs and in microbial communities are expected to affect SOC formation and turnover (Conant *et al* 2004).

While SOC tends to be greater in irrigated systems, it is unclear whether SOC-related soil functions can be maintained, including related soil microbial dynamic changes following irrigation retirement. Because soil moisture will decrease and a strong decrease in crop production is expected due to water limitation following irrigation retirement, a decline in resource availability and changes in microbial community composition and activity are expected (Manzoni *et al* 2012, Fuchslueger *et al* 2014, Ma *et al* 2015, Cano *et al* 2018). In semiarid climates where moisture is often a limiting factor or under drought, soil moisture is usually positively correlated with microbial biomass and activity (Sardans *et al* 2008, Pérez-Guzmán *et al* 2020), but there are also reports of microbes being unresponsive to drought (Canarini *et al* 2016) or even increases in microbial biomass during summer droughts (Schaeffer *et al* 2017). Differential responses of specific extracellular enzymes to moisture are also reported (Sardans *et al* 2008, Alster *et al* 2013, Ren *et al* 2017) making it difficult to predict general changes. In addition, crop selection and substrate availability can condition microbial responses to irrigation retirement. For example, the transition from a low residue irrigated crop such as cotton to high biomass-producing sorghum may result in an increase in microbial biomass and enzyme activity, even after irrigation retirement in semiarid climates (Cotton *et al* 2013). Moreover, because plants tend to produce proportionally more roots than shoots in response to drought (Zhou *et al* 2018) substrate availability for microorganisms may be less affected than crop productivity. Thus, although it can be expected that irrigation retirement would have a negative impact on biomass production and soil microbial communities, it is hard to anticipate the magnitude of these effects.

Our objective was to compare the impact of the transition from irrigated to dryland cropping systems on crop production and soil microbial dynamics under the two major crops of the semiarid High Plains. To do this, we installed a transition experiment to quantify crop production, biomass partitioning, soil microbial biomass, community composition, and activity, between irrigated and non-irrigated (retired) treatments for three years in two cropping systems: continuous maize and continuous winter wheat. Because winter wheat is more adapted to the climate of this area (Farahani *et al* 1998, Hansen *et al* 2012), we hypothesized that dryland wheat would be a better option than dryland maize, but that dryland wheat still may not maintain soil health compared to the baseline irrigated system. This information will help to anticipate longer-term changes in SOC and soil function that may take place across the landscape with larger scale irrigation retirement.

2. Materials and methods

2.1. Field management and experimental design

The experiment was conducted at the Agricultural Research Development and Education Center of Colorado State University near Fort Collins (40°39'16"N, 104°59'55"W; 1555 m a.s.l.). The climate at the site is characterized by an annual precipitation of 408 mm, with an average annual temperature of 10.2 °C (1981–2010 average, <https://usclimatedata.com/>). The selected field was historically used for irrigated crop production managed with conventional tillage. The last tillage operation was conducted in April 2017, before installing the experiment. The soil is classified as an Aridic Haplustalf (USDA, NRCS 2019), and the textural class was defined as a sandy clay loam (54% Sand, 14% Silt, 32% Clay). At the beginning of the experiment the soil had a bulk density of 1.26 g cm⁻³ and pH was 8.1.

In this formerly irrigated field, we initiated a factorial experiment with four treatments, consisting of all combinations of two crops (maize and winter wheat) and two water managements (irrigated and dryland) in a randomized complete block design with four replicates. Plots measured 48 × 14 m for maize and 24 × 14 m for wheat. As we were interested in the transition from irrigated to dryland under each continuous crop, the irrigated treatments represented controls.

The experiment was started in May 2017 at maize planting. Maize (*Zea mays*) was planted around mid-May and winter wheat (*Triticum aestivum*) between late September and early October. Wheat was harvested in July and maize was harvested in September–October. During the experiment all the treatments were managed using no-till practices, so the studied changes include both the effect of irrigation retirement and no-till adoption. Soil samples were taken at the beginning and end of each growing season, in late spring and fall. Final samples were collected in November 2019, after three maize and two wheat seasons.

Each crop was managed following local recommendations of seeding and fertilization rates. These recommendations differ based on water management and, because our objective was to compare a typical irrigated versus dryland cropping system, we adjusted the agronomic management of each crop to each water management situation. Therefore, given the high effect of plant density and nitrogen management on cereal yields (e.g., Ciampitti and Vyn 2012, Bhatta *et al* 2017), our treatment effects represent holistic differences between irrigated and dryland crop management systems and cannot be attributed to differences in water availability alone. For maize, the Producers Hybrids 5218 SSTX was planted in 0.76-m rows at 84,000 and 42,000 seeds ha⁻¹ for irrigated and dryland, respectively. Avery wheat was planted at 100–110 and 60–70 kg seed ha⁻¹ for irrigated and dryland, in 0.19-m rows. Fertilization rates were defined based on standard soil test results from the Soil, Water and Plant Testing Laboratory at Colorado State University, and monoammonium phosphate (11-52-0) and urea (46-0-0) were broadcasted during early stages of crop development. On average, irrigated maize received 165 kg N ha⁻¹ and 50 kg P₂O₅ ha⁻¹ and dryland maize received 90 kg N ha⁻¹ and 40 kg P₂O₅ ha⁻¹, annually. Wheat was fertilized with 50 kg N ha⁻¹ and 22 kg P₂O₅ ha⁻¹ the first year for both treatments, and no fertilization was required on the second year based on soil test results. Pre- and post-emergence herbicide applications were used for weed control.

For the irrigated treatments irrigation was done once per week, usually on Tuesdays, from May to September for Maize. Wheat was irrigated from May to June–July, and in 2018 it was irrigated twice after planting at the end of September. Weekly irrigation amounts were managed at the farm level for various fields at the same time, and were defined based on moisture conditions, crop phenology, and weather forecast. Precipitation and reference evapotranspiration (Kimberly Penman alfalfa reference equation) data was recorded in a weather station from the Colorado Agricultural Meteorological Network located inside our research station (CSU-ARDEC, ftc03). To characterize crop water availability in each season, we estimated the water balance for each crop in the experiment using the WISE Irrigation Scheduler (<http://wise.colostate.edu/>) developed by Andales *et al* (2014).

2.2. Crop sampling

We quantified the effect of irrigation retirement on above- and belowground biomass production of each crop. Belowground biomass determination was done at flowering of each crop. Using a Giddings soil probe with a 6.5-cm diameter core we took four samples per plot, two in the crop row and two between the rows, and divided the samples by depth (0–10, 10–20, 20–40, 40–60, and 60–80 cm). Samples were kept in coolers before going back to the lab, where samples were refrigerated until root washing. Each sample was soaked in water and passed through three sieves of 2.0 mm, 1.0 mm, and 0.5 mm, and the roots were recovered using tweezers. Recovered roots were rinsed, oven-dried at 55 °C–60 °C for at least 48 h and weighed. We accounted for the sampled area and averaged the in-row and between-row samples to estimate belowground dry matter per hectare at each sampling depth. Two exceptions to this protocol were for Maize 2017, when it was impossible to sample below 60 cm, and for Maize 2019, when root recovery was affected by a failure in the root washing procedure that resulted in the loss of many samples. To overcome this problem, we estimated root biomass for Maize 2019 at

crop harvest during soil sieving to 8 mm without soaking the sample in water. Thus, the estimation of root biomass on this last crop is composed mainly of coarse roots and presented as total biomass per area, as we did not record the root distribution by depth.

Total aboveground biomass production was measured at physiological maturity of each crop by sampling two representative sub-areas from the center of each plot. We sampled a total area of 9.12 and 4.56 m² for maize and wheat plots, respectively, weighed the entire sample and separated the grain from the stover. A representative subsample of each component was oven-dried at 55 °C–60 °C for at least 48 h to calculate total dry matter from fresh weights. To compare the productivity between crops, we assumed than mean caloric content was 356 kcal per 100 g for maize grain and 335 kcal per 100 g of grain for wheat (FAO 2001). We used the line-transect method (Laflen *et al* 1981) to estimate soil residue cover in the maize plots at planting and harvest of the second and third year.

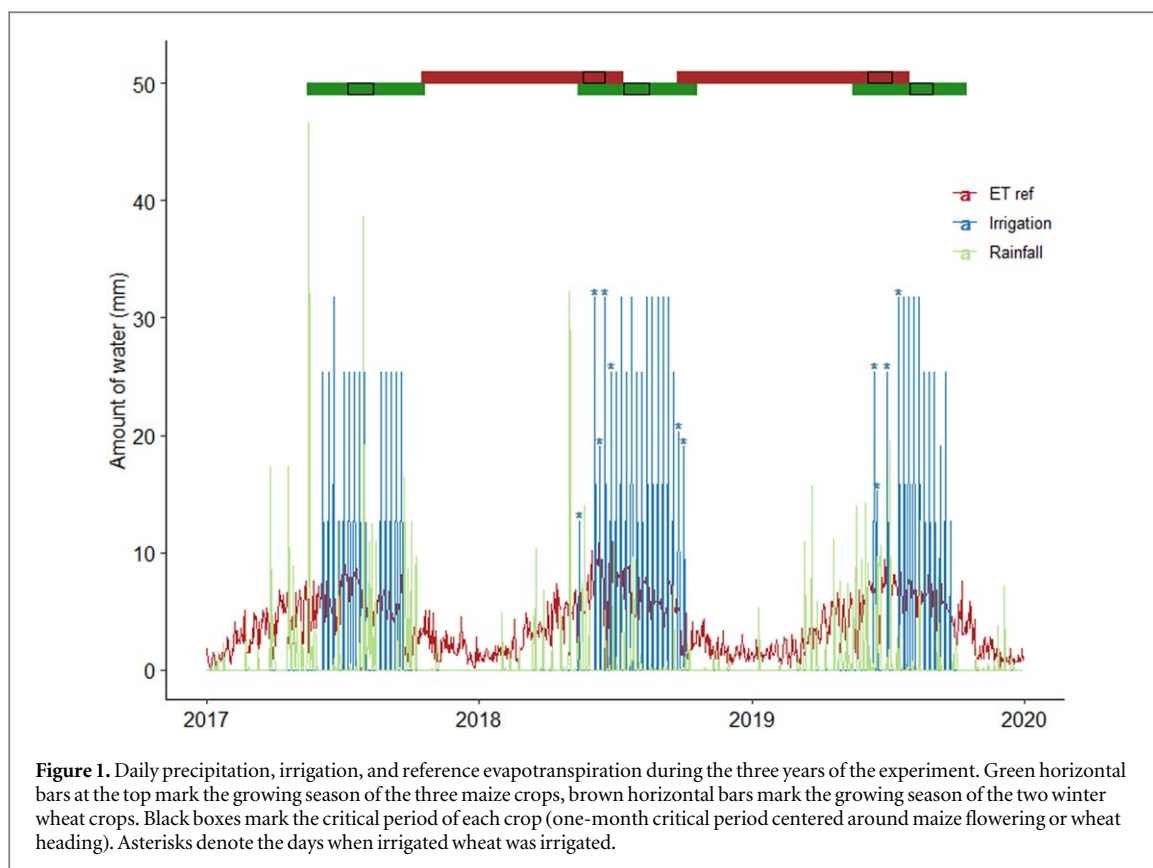
2.3. Soil sampling and analysis

To assess soil microbial responses to irrigation retirement and crop selection, we used phospholipid fatty acids as markers of microbial abundance and community composition, and extracellular enzyme assays (at the final sampling) as a proxy of potential microbial activity. We also analyzed gravimetric water content and salt-extractable carbon and nitrogen to understand the changes in soil moisture and substrate availability that may influence soil microbial communities. We collected soil samples for microbial community analysis twice a year, in spring (May–June) and fall (October–November). We took 15–20 2-cm diameter soil cores, avoiding the borders of each plot. Cores were composited by plot and depth, placed in plastic bags, stored in coolers, and transported to the lab, where they were refrigerated for 1–2 weeks until sample processing and analysis. Soil samples were taken at two depths (0–10 and 10–20 cm), but due to the low treatment effects found in the surface samples, and the similar evolution of soil moisture and nutrient availability at both depths, we only conducted PLFAs and enzyme analyses on the surface samples.

To estimate soil gravimetric water content of each sample, a 10 g subsample was oven-dried at 105 °C for 48 h and reweighed. To quantify the availability of organic C and N, 20 g soil samples were shaken for 4 h at 75 rpm in 100 ml of 0.5 M K₂SO₄, centrifuged 10 min, and filtered through 0.45 μm filters. The extracts were analyzed for organic C and total N with a TOC-V-TN analyzer (Shimadzu Corp., Kyoto, Japan). We used colorimetric analyses to determine nitrate and ammonium concentrations in the extracts (Sims *et al* 1995, Doane and Horváth 2003). Ammonium concentrations were below the detection limit in almost 90% of the samples so only nitrate results are presented as an estimation of the proportion of inorganic N.

Phospholipid fatty acids were used to characterize microbial biomass and community composition at 0–10 cm depth. For their extraction, a subsample of fresh soil was sieved to 2 mm, cleaned of roots, lyophilized and sent to Ward Labs (Lincoln, Nebraska, US). Based on Hamel *et al* (2006) lipids were extracted by shaking 2 g lyophilized soil with 9.5 ml of a 1:2:0.8 v/v/v dichloromethane (DCM)/methanol/citrate buffer solution for 1 h. Then, 2.5 ml of DCM and 10 ml of a saturated KCl solution were added, shaken for 5 min and centrifuged to remove the organic fraction. Phospholipids were isolated in solid phase extraction columns using methanol, after eluting the neutral fatty acids and glycolipids with DCM and acetone. Phospholipids were then methylated with 2 ml of MeOH/H₂SO₄ and 2 ml of hexane and quantified by gas chromatography on an Agilent 7890A GC (Agilent, California, US). We used the PLFA 18:2ω6 as a fungal biomarker and the following PLFAs as bacterial biomarkers: i14:0, i15:0, a15:0, 15:0, i16:0, 16:1ω7c, i17:0, a17:0, 17:0, 17:1ω8c, 18:1ω7c, 18:1ω5c, 10Me16:0, 10Me17:0, and 10Me18:0 (Frostegård *et al* 1993, Frostegård and Bååth 1996, Zelles 1999). Bacterial PLFA biomarkers were divided into gram-positive (i14:0, i15:0, a15:0, i16:0, i17:0, a17:0), gram-negative (16:1ω7c, 17:1ω8c, 18:1ω7c, 18:1ω5c), and actinomycete (10Me16:0, 10Me17:0, 10Me18:0) functional groups.

For the last sampling, in Fall 2019, we also measured the potential activity of six soil enzymes related to cellulose degradation (β -D-cellobiohydrolase and β -glucosidase), protein degradation (L-leucine aminopeptidase and tyrosine aminopeptidase), chitin degradation (β -1,4-N-acetyl-glucosaminidase), and phosphorous mineralization (acid phosphatase). To explore whether the effect of irrigation on microbial activity was only a transient effect due to differences in water availability at sampling or whether treatment effects persisted when moisture was equalized, we compared extracellular enzyme activity in fresh and air-dry soil samples. Thus, each sample was analyzed twice, at field moisture conditions (no more than a week after sampling) and after air-drying the samples for ~2 weeks. Following the protocol of Saiya-Cork *et al* (2002) soil slurries were made by homogenizing 1 g of each sample in approximately 120 ml of 50 mM, pH 8.1, tris buffer. Then, 200 μl of each slurry was pipetted into black, 96-well microplates and mixed with 50 μl of 200 μM substrate. Slurries were also mixed with buffer only or with the corresponding standards (10 mM 4-methylumbelliferone, or 7-amino-4-methyl coumarin) as negative and quenching controls, respectively. Samples were incubated at 25 °C for 4 h and the developed fluorescence read on a microplate reader (Cytation 5, BioTek, Vermont, USA) at 365 nm excitation and 450 nm emission wavelengths.



2.4. Statistical analyses

Data exploration and statistical analyses were conducted in R version 3.6.3 (R Core Team 2020), with the packages *car* (Fox and Weisberg 2011), *lme4* (Bates *et al* 2015), *lmerTest* (Kuznetsova *et al* 2017), and *emmeans* (Lenth *et al* 2018). For the statistical analyses of the results, we consider the factorial design of two water managements (irrigated or dryland) and two crop types (maize and wheat), arranged in a randomized complete block design with four replicates.

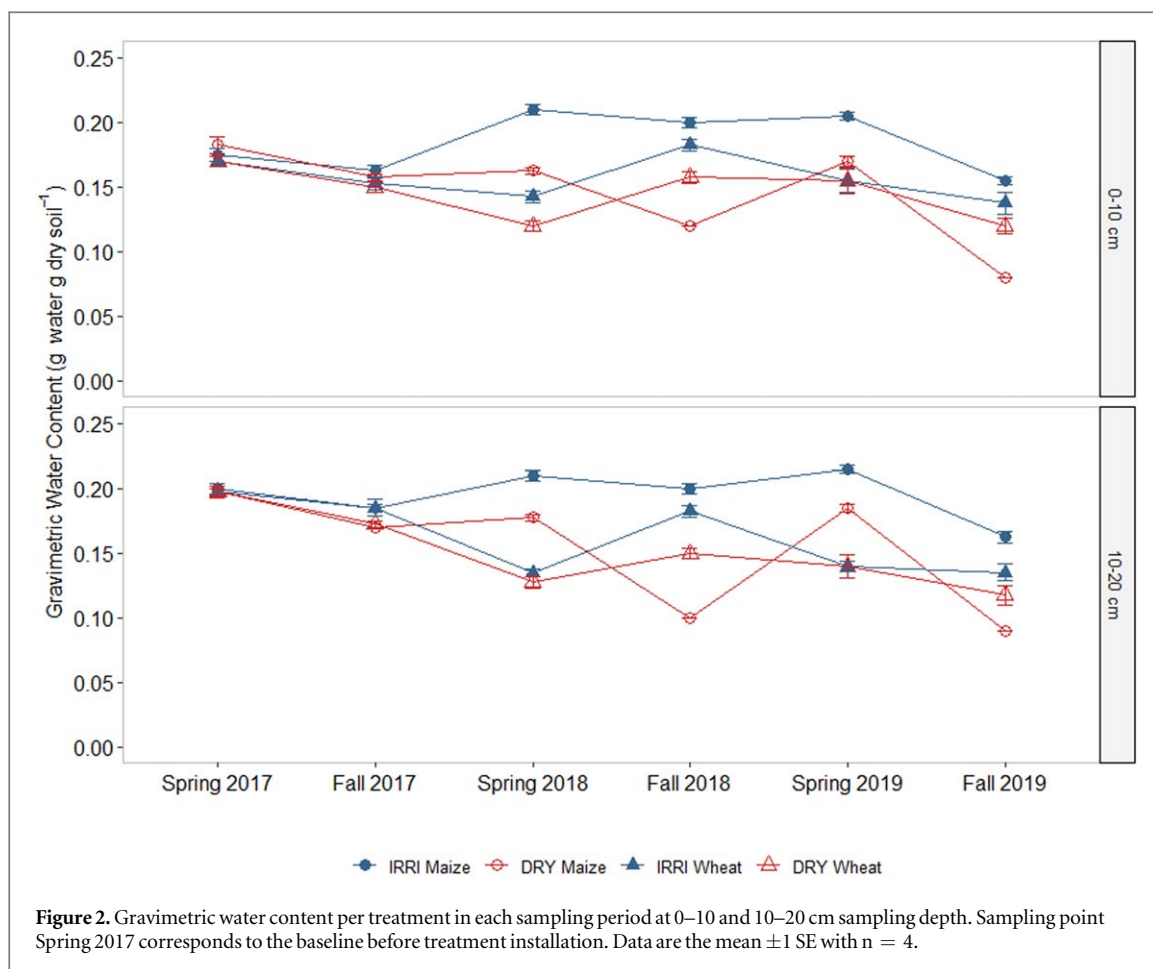
For the different components of biomass production, we included water management, crop type, and their interaction as fixed effects, and block as random effect, in a *lmer* mixed model. We also explored root distribution for each crop, but we only found an interaction between water management and depth on maize 2018 so we focused mainly on total root production. The significance of all fixed effects and their interactions were tested by Type III analysis of variance with Kenward-Roger's method. When fixed effects were significant ($P < 0.05$ unless otherwise noted in the text) means were compared using Tukey adjusted pairwise comparisons.

For the soil variables measured seasonally, we included sampling as an extra fixed effect and a random term representing each experimental unit (plot) to consider the repeated measurements design. In Fall 2017, the baseline sampling, we only sampled three plots per block, as only three treatments were planned at that time. Because of this, the baseline sampling was analyzed separately and not considered in the repeated measurement analysis of soil variables. In addition, changes in microbial community composition were explored by non-metric multidimensional scaling (NMDS) of the PLFA data with the *vegan* package (Oksanen *et al* 2020). For the analysis of enzyme activity in Fall 2019, the model included the effect of sample handling (fresh versus air-dried) and the interactions with water management and crop type.

3. Results

3.1. Seasonal water dynamics

Precipitation varied both between and within years, with differences in total rain amounts and in the distribution of rain events during the growing seasons (figure 1). Atmospheric demand also varied between years (figure 1), but it was more stable than precipitation, and reference evapotranspiration during the experimental period was very similar to the long-term average (figure S1 available online at stacks.iop.org/ERC/4/035004/mmedia). Accumulated precipitation was highest in 2017 and lowest in 2018, but 2019 was the year with the lowest precipitation during the critical period for maize yield. Total rain during the critical period of one month



around maize flowering (Otegui *et al* 1995) was 85 mm, 33 mm, and 14 mm for the years 2017, 2018, and 2019, respectively. During the same period, accumulated reference evapotranspiration was 189, 203, and 187 mm, resulting in better conditions for dryland maize production in 2017 and higher water deficits in the following growing seasons. These differences in seasonal weather resulted in differences in water management and moisture availability during the different growing seasons (figures 1 and S1). Total irrigation in maize was between 350 and 495 mm annually, which resulted in irrigated maize receiving two to five times more water than the corresponding dryland treatment. With this irrigation management we were able to maintain higher and more stable levels of plant available water (figure S1), and estimated water consumption was on average 2.5 times higher in the irrigated than in the dryland treatment (table S1).

Between winter wheat planting and harvest, total precipitation was 181 mm in 2017–2018 and 253 mm in 2018–2019, and there were also differences in rainfall distribution during wheat critical period of one month around heading (Fischer 1985, Abbate *et al* 1995). During the critical period of 2018, total precipitation was 21 mm and reference evapotranspiration was 206 mm, while during the 2019 growing season there were 71 mm of accumulated rainfall and 202 mm of reference evapotranspiration (figure 1). Plant water availability did not limit wheat growth during the spring (figure S1), and most of the irrigation in this crop occurred in late spring and early summer (figure 1). Irrigated wheat received 50%–80% more water than the dryland wheat (141 mm average per crop), which resulted in different plant water availability during the reproductive stages of the crop. These differences in plant water availability increased crop water use by 15% in the irrigated compared to the dryland wheat treatment (table S1).

The seasonal evolution of soil moisture reflected the differences in precipitation, irrigation management, and growing seasons (figure 2). Maize treatments consumed water mainly during the summer, and soil moisture recovered during the winter, while in wheat plots the recovery of soil moisture occurred after crop maturity in early summer. Irrigation increased soil moisture throughout the experiment, with a higher effect on maize than on wheat as expected due to the more intense irrigation management. Compared to irrigated maize, all the other treatments had lower soil moisture with higher seasonal variability. Gravimetric water content at flowering of each crop confirmed the observed seasonal patterns, with differences due to irrigation increasing each growing season (figure S2). In the first crop after irrigation retirement, the differences at flowering were concentrated in the 0–20 cm layer, but in the following crops irrigation effect on soil moisture was consistent in the entire profile

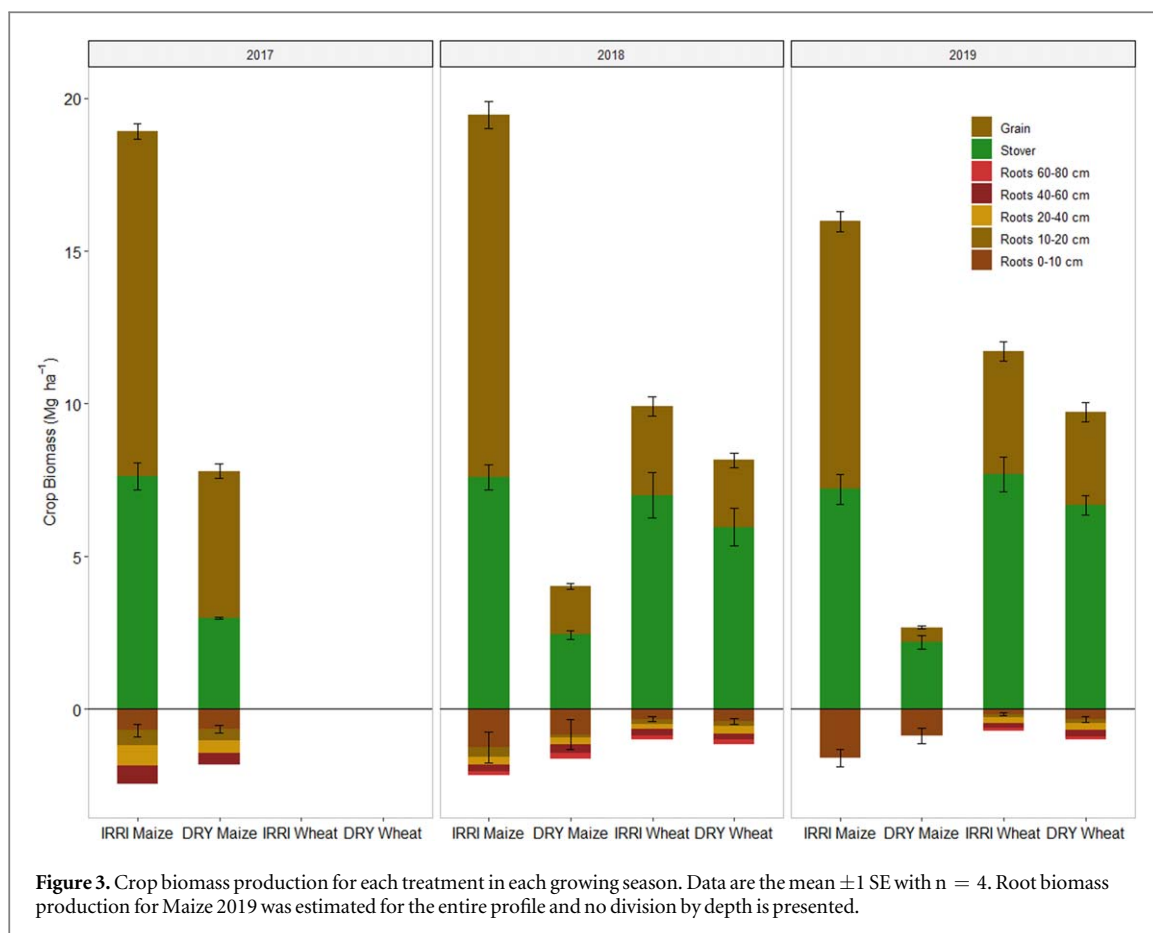


Figure 3. Crop biomass production for each treatment in each growing season. Data are the mean \pm 1 SE with $n = 4$. Root biomass production for Maize 2019 was estimated for the entire profile and no division by depth is presented.

(0–80 cm). We did not observe an important irrigation effect after the first maize crop, in fall 2017, due to late season rain events that recovered soil moisture after the peak of plant water consumption. However, during flowering at the end of July 2017 irrigated maize had 30% more gravimetric water content than the dryland treatment at 20 cm depth (0.15 versus 0.12 g water g dry soil⁻¹).

3.2. Crop biomass production

Crop response to irrigation treatment varied by crop and plant component (figure 3). Irrigation retirement strongly affected maize production with 2 to 6-fold decreases in total aboveground biomass production and even stronger decreases in grain yield in dryland relative to irrigated maize. After three growing seasons, average grain yield was 10.6 Mg ha⁻¹ crop⁻¹ for irrigated compared to 2.3 Mg ha⁻¹ crop⁻¹ for dryland maize. The effect of irrigation on winter wheat production was lower than on maize and statistically significant only in 2019, with a stronger effect on grain yield than on biomass production (30% versus 20% increase). Irrigated maize had the highest biomass production, mostly explained by the high grain yield. Aboveground residue production was similar between irrigated maize and both wheat treatments, and lowest in the dryland maize. Under dryland conditions wheat was more productive than maize, with 13% higher grain yield and 90% more residue production per crop. The large differences in aboveground maize production resulted in differences in soil cover, with irrigated maize having twice the soil cover than dryland (table 1).

The irrigation effect on root production was lower than on aboveground biomass. There was 40%–80% less belowground biomass in dryland than in irrigated maize, but in 2018 the difference was significant only at 0–10 and 10–20 cm (figure 3). Across both years, dryland wheat had almost 20% more belowground biomass than the irrigated treatment, but the difference was not statistically significant. There was also a crop effect on belowground biomass ($p < 0.05$), as wheat produced lower root biomass than maize (figure 3). Irrigation retirement increased the root to shoot ratio, and the effect was again higher in maize than in wheat (table 2). The average root to shoot ratio was 2.7 times higher in dryland than in irrigated maize and 1.5 times higher in dryland than irrigated wheat.

3.3. Soil microbial responses to irrigation retirement

Neither irrigation nor crop type had clear effects on dissolved organic C and N availability. Salt-extractable C varied mainly in response to sampling season at both depths (figure 4, table 3). There were differences between

Table 1. Percent of soil cover in the maize treatments at the planting of the second crop (Spring 2018), harvest of the second crop (Fall 2018) and planting and harvest of the third crop (Spring and Fall 2019). P-values correspond to the treatment effect from the type III ANOVA with Kenward-Roger's method.

		Spring 2018	Fall 2018	Spring 2019	Fall 2019
Irrigated Maize	Mean \pm SE	77 \pm 4.2	98 \pm 0.9	92 \pm 1.0	99 \pm 0.3
	CV (%)	10.9	1.8	2.2	0.6
Dryland Maize	Mean \pm SE	25 \pm 5.3	63 \pm 2.9	35 \pm 2.7	57 \pm 2.8
	CV (%)	41.7	9.3	15.3	9.9
p-value		0.005	0.001	<0.001	<0.001

Table 2. Irrigation effect on root to shoot ratio of each crop. Data are the mean \pm 1 SE with n = 4; p-values correspond to the fixed effects of water management, crop type, and their interaction from the type III ANOVA with Kenward-Roger's method.

Treatment	2017	2018	2019
Root: Shoot ratio			
Irrigated Maize	0.14 \pm 0.01	0.12 \pm 0.02	0.10 \pm 0.02
Dryland Maize	0.23 \pm 0.02	0.40 \pm 0.12	0.35 \pm 0.12
Irrigated Wheat	—	0.11 \pm 0.02	0.06 \pm 0.00
Dryland Wheat	—	0.15 \pm 0.01	0.10 \pm 0.02
p-values			
Water	0.010	0.005	0.002
Crop	NA	0.035	0.001
Water:Crop	NA	0.078	0.061

treatments in the concentration of total salt-extractable N, but they were explained mainly by the accumulation of nitrate, which was highest in the wheat plots in Fall 2017 and in the dryland maize treatment in the last three samplings (figure 4). Moreover, there was an accumulation of inorganic N during the growing season and a loss during the winter fallow, as nitrate concentrations were higher in the fall than in the spring samplings. The results at the 10–20 cm depth were consistent with the observations at surface.

Soil microbial biomass and total bacteria, assessed by PLFA, increased during the experimental period, with the highest values found in the last sampling (figure 5). Across samplings and crops, there was a tendency for both indicators to be higher under irrigation (table 3), but the tendency was not consistent over time. The response of the functional groups evaluated was similar, and the non-metric multidimensional analysis showed no differences in microbial community composition associated to either treatment or sampling time (figure S2). The concentration of the PLFA 18:2 ω 6 (only marker used as a fungal biomarker) was always very low, representing less than 2% of the total microbial PLFAs identified, and it also increased over time across all treatments (figure 5c).

There was a significant effect of irrigation and crop type on the activity of the six extracellular enzymes evaluated, which were more often affected by irrigation retirement in maize than in wheat (figure 6, table 4). Enzyme activity was correlated with gravimetric water content ($r = +0.46$ to $+0.71$), and air drying the samples decreased estimated activity in all the enzymes, but the proportional decrease was higher in the irrigated than in the dryland treatments (fresh:dry ratio was 1.64 for irrigated maize, 1.43 for dryland maize, 1.50 for irrigated wheat, and 1.31 for dryland wheat). This resulted in different interpretations of the irrigation effect depending on sample handling. When the assays were conducted using fresh samples, irrigation retirement decreased the activity of β -glucosidase, β -D-cellobiohydrolase, β -1,4-N-acetyl-glucosaminidase, and acid phosphatase ($p < 0.01$ in all cases), but after air-drying the effect was significant only for β -1,4-N-acetyl-glucosaminidase. For some enzymes, the effect of irrigation retirement also varied by crop type. The activity of L-leucine aminopeptidase and tyrosine aminopeptidase decreased after irrigation retirement in maize but increased after irrigation retirement in wheat. Irrigation retirement decreased the activity of acid phosphatase in maize but did not differ between wheat treatments.

While sample air-drying affected water treatment differences in enzyme activity, it did not affect the estimation of crop effect on any of the enzymes (table 4). The carbon cycling enzymes β -glucosidase and β -D-cellobiohydrolase had higher activity in wheat than in maize treatments, consistent across irrigation

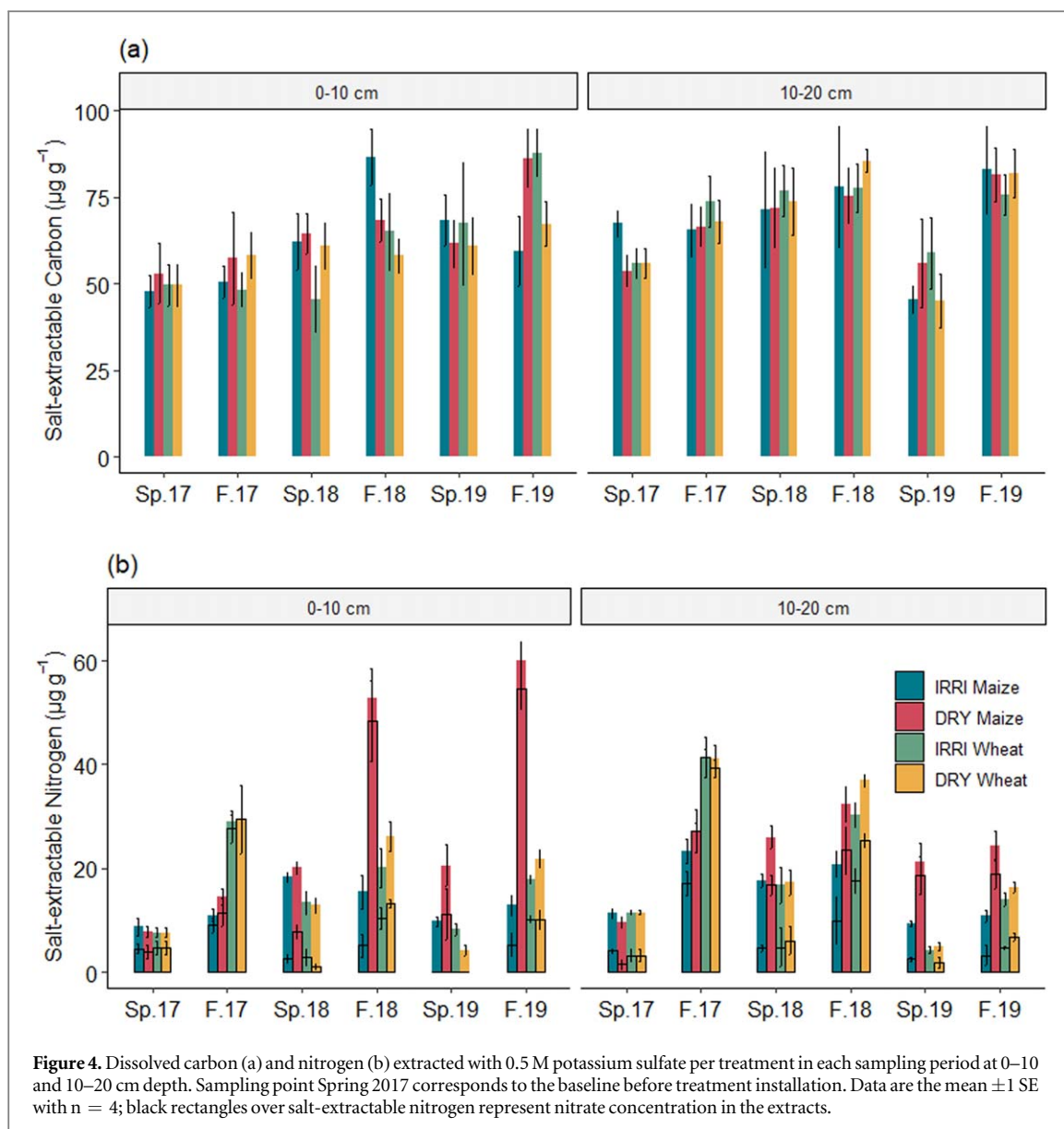
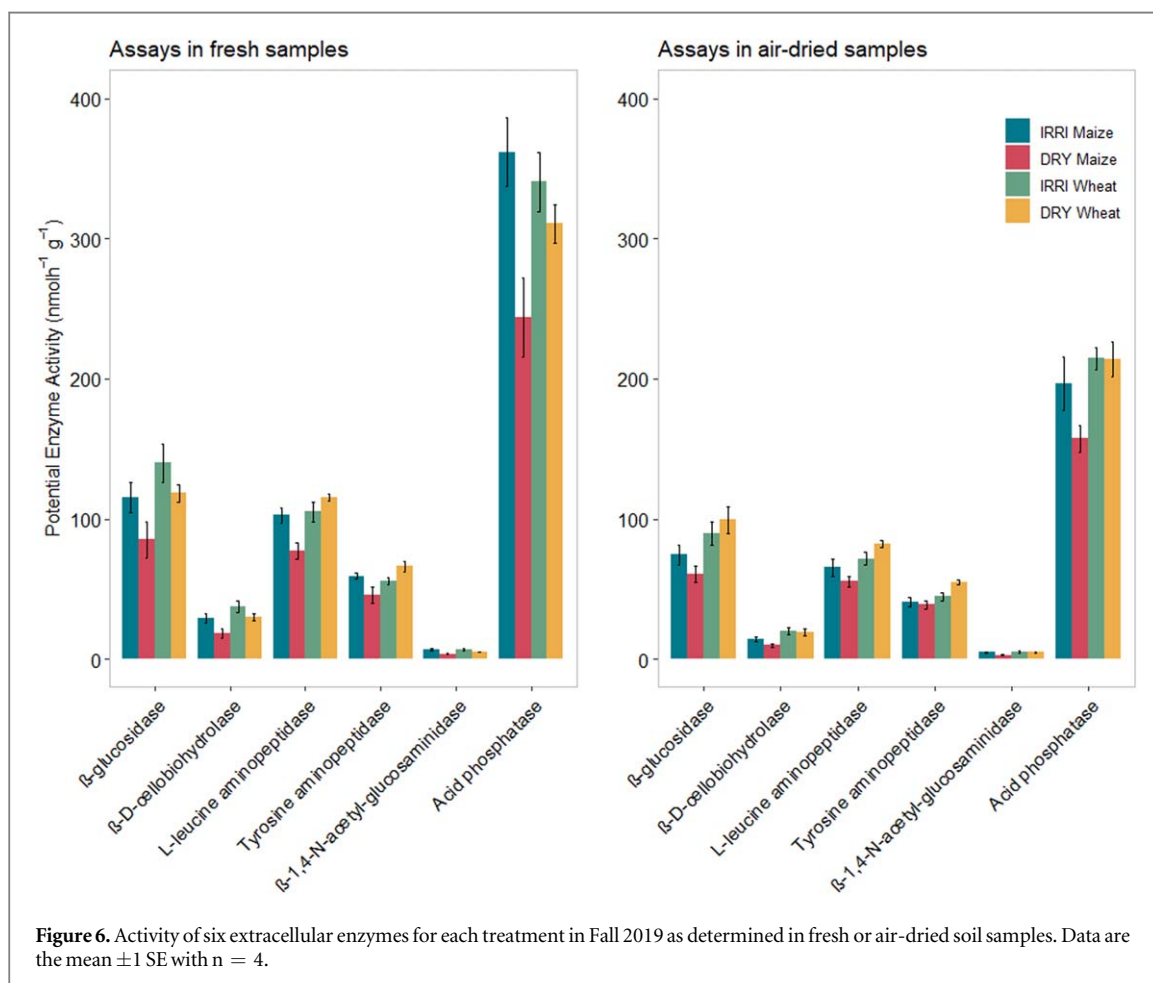
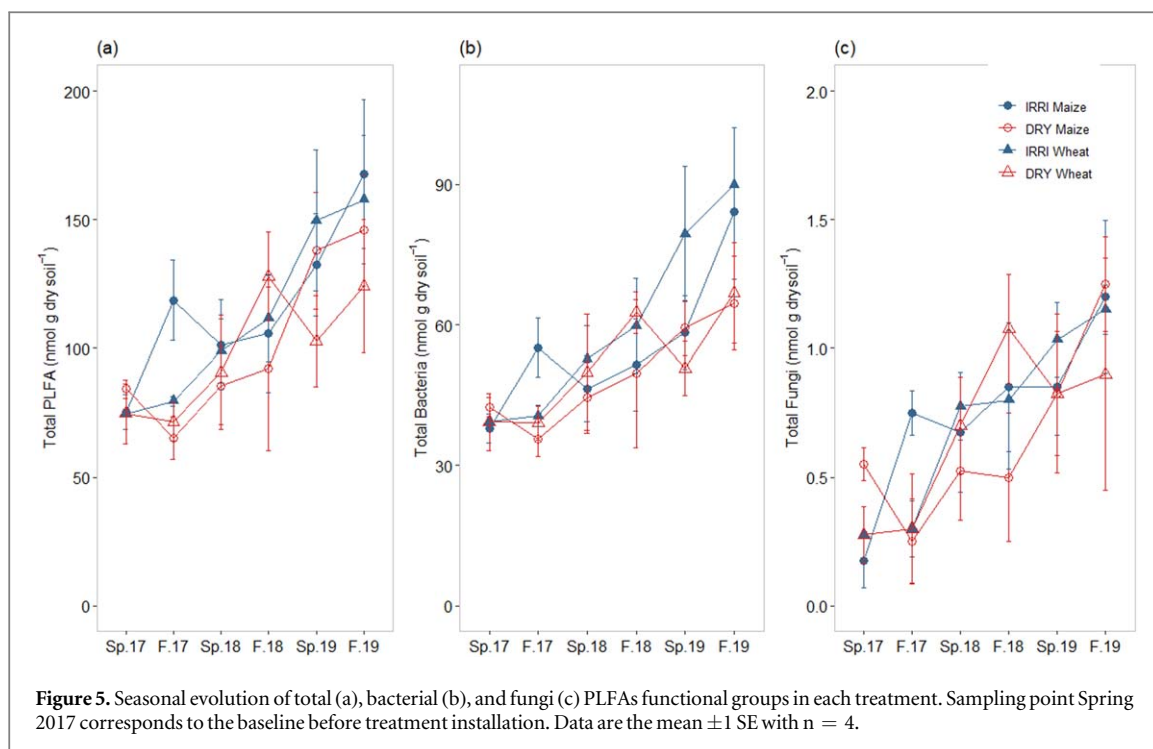


Figure 4. Dissolved carbon (a) and nitrogen (b) extracted with 0.5 M potassium sulfate per treatment in each sampling period at 0–10 and 10–20 cm depth. Sampling point Spring 2017 corresponds to the baseline before treatment installation. Data are the mean ± 1 SE with $n = 4$; black rectangles over salt-extractable nitrogen represent nitrate concentration in the extracts.

Table 3. Treatment effects on the seasonal measures of salt-extractable organic C and total N at 0–10 and 10–20 cm, and biomass of main microbial groups assessed by phospholipid fatty acids at 0–10 cm. P-values of fixed effects from the Type III analysis of variance with Kenward-Roger’s method.

Factor	df	0.5 M K ₂ SO ₄ Extractable Carbon		0.5 M K ₂ SO ₄ Extractable Nitrogen		Phospholipid Fatty Acids		
		0–10 cm	10–20 cm	0–10 cm	10–20 cm	Total	Bacteria	Fungi
Sampling	4	0.002	<0.001	<0.001	<0.001	<0.001	<0.001	0.001
Water management	1	0.948	0.932	<0.001	<0.001	0.099	0.106	0.299
Crop	1	0.226	0.558	<0.001	0.408	0.706	0.445	0.875
Sampling:Water	4	0.212	0.988	<0.001	0.097	0.789	0.541	0.973
Sampling:Crop	4	0.351	0.934	<0.001	<0.001	0.657	0.832	0.475
Water:Crop	1	0.591	0.667	<0.001	0.011	0.854	0.833	0.536
Sampling:Water:Crop	4	0.047	0.450	<0.001	0.423	0.459	0.546	0.505

management. The other enzymes, involved in nitrogen and phosphorus cycling, were higher in dryland wheat than in dryland maize, but did not differ between crop type when irrigation was applied. The activities of L-leucine aminopeptidase and tyrosine aminopeptidase were also higher in dryland wheat than in irrigated maize.



4. Discussion

We quantified the effect of irrigation retirement on plant production and soil microbial communities under the two main crops of the Great Plains, maize and wheat. Our results suggest that the expected increase in dryland

Table 4. Effects of treatment and sample handling on extracellular enzyme activities. P-values of fixed effects from mixed effects model, Type III analysis of variance with Kenward-Roger’s method.

Factor	df	β -glucosidase	β -D-cellobiohydrolase	L-leucine aminopeptidase	Tyrosine aminopeptidase P-value	β -1,4-N-acetyl-glucosaminidase	Acid Phosphatase
Water	1	0.027	0.005	0.266	0.570	<0.001	<0.001
Crop	1	<0.001	<0.001	<0.001	0.001	0.005	0.004
Air-drying	1	<0.001	<0.001	<0.001	<0.001	0.001	<0.001
Water:Crop	1	0.187	0.342	<0.001	0.001	0.051	0.003
Water:Air-drying	1	0.055	0.081	0.238	0.272	0.044	0.009
Crop:Air-drying	1	0.871	0.524	0.583	0.734	0.675	0.444
Water:Crop:Air-drying	1	0.524	0.986	0.252	0.228	0.994	0.206

wheat under water scarcity (Farahani *et al* 1998, Hansen *et al* 2012, Cano *et al* 2018) is a viable option not only to sustain crop production but also to minimize the negative impacts of irrigation retirement on soil health. Lower soil moisture after irrigation retirement decreased plant biomass production in both crops, with a higher effect on maize than on wheat. Despite large changes in soil moisture and plant biomass production, the effect of irrigation retirement on soil microbial community size and composition was limited. However, soil microbial activity was affected by irrigation retirement, again with a greater effect on maize than on wheat. Biomass allocation was also affected by irrigation retirement, as aboveground biomass production was more affected than roots, changing the distribution of C inputs to the soil. While transitioning to dryland wheat might help maintain surface residues, the lower root production of wheat relative to maize may affect the efficiency of SOC formation.

4.1. Crop responses to irrigation retirement

Irrigation retirement decreased total crop production and shifted biomass allocation patterns toward belowground in both crops, with more extreme effects on maize. Maize has higher water requirements than most crops in the region (Lamm *et al* 2007, Araya *et al* 2017, 2019) and it was strongly affected by irrigation retirement. Averaged over the three seasons, the maize yield reduction due to irrigation retirement was $8.3 \text{ Mg ha}^{-1} \text{ crop}^{-1}$, which is higher than the long-term irrigation-limited yield gap of 6.0 to 7.5 Mg ha^{-1} reported for this county (Kukul and Irmak 2019). Our higher estimations of irrigation-limited yield gaps were related to the very low yields in the dryland treatment during 2018 and 2019 (figure 3). Interannual variability in summer rainfall explains the high differences in the yield of dryland maize across the three years, because this crop is highly susceptible to drought stress during the reproductive stage that occurs during the summer months when evaporative demand is highest (Sherrod *et al* 2014).

In the Great Plains there is an east-west precipitation gradient, with a mean annual precipitation of more than 500 mm on the eastern boundary of the semi-arid zone where dryland maize is more commonly grown (Hansen *et al* 2012). This is almost 100 mm more precipitation than the climatic average of our experimental site and 200 mm higher than the annual precipitation during the experimental period, but still less than the total amount of water added with irrigation. Consequently, estimated yield gaps between irrigated and dryland crops decrease to the east, following the precipitation gradient (Kukul and Irmak 2019), which indicates that yield penalties due to irrigation retirement would be lower on the eastern boundary of the Great Plains. Thus, our results can be considered as an extreme example of the potential impacts of irrigation retirement on crop production for the Central High Plains area of the Ogallala Aquifer. However, high variability in precipitation is a characteristic of the Great Plains (Hansen *et al* 2012), and dryland maize is an important dryland rotation crop even in parts of the region with mean annual precipitation below 500 mm (Rosenzweig and Schipanski 2019).

Winter wheat, on the other hand, is well adapted for dryland production in the Great Plains because it uses the water accumulated during cooler fall and spring months and matures before the hot and dry late summer conditions (Hansen *et al* 2012). This results in lower yield responses to irrigation ($1\text{--}2 \text{ Mg ha}^{-1}$, Kukul and Irmak 2019), and explains the performance of this crop after irrigation retirement, with differences in grain yield due to irrigation of only 30% ($0.9 \text{ Mg ha}^{-1} \text{ crop}^{-1}$) while maize yield was at least doubled by irrigation. Although winter wheat is a viable option to maintain crop productivity under water scarcity, the transition from irrigated maize to dryland wheat resulted in a high decrease in productivity. Annual calorie production was more than four times higher in irrigated maize than in dryland wheat (37.9 versus $8.7 \times 10^6 \text{ kcal ha}^{-1} \text{ crop}^{-1}$), highlighting the net loss of productivity after irrigation retirement. However, maize is primarily used for feeding livestock whereas wheat is directly consumed by humans, making it difficult to anticipate the net system-wide effect of this transition on food production.

Biomass production and the amount of crop residues returning to the soil impact the evolution of SOC stocks (Halvorson and Schlegel 2012, Halvorson and Stewart 2015). After irrigation retirement the production of crop residues in maize was very low, but dryland wheat had levels of residue input per crop similar to irrigated maize. Thus, wheat appears as a more viable option than maize to maintain the levels of surface residues during the transition from irrigated to dryland cropping systems. However, both irrigation retirement and crop type affected the distribution of crop residues and the proportion of roots. Root production plays a key role in carbon inputs because roots form proportionally more SOC than aboveground biomass residues (Rasse *et al* 2005, Mazzilli *et al* 2015, Fulton-Smith and Cotrufo 2019). The higher root:shoot ratio in the dryland treatments may partially offset the negative impact of less crop production on SOC and might explain the lower than expected differences in soil microbial communities between irrigation treatments. But dryland maize produced almost 2.5 times less crop residue mass than irrigated maize. Thus, our results suggest that while shifts in biomass allocation belowground may reduce the rate of SOC depletion with irrigation retirement, the larger gross reduction in ecosystem net primary productivity with irrigation retirement will contribute to reduced SOC over time. A transition from irrigated maize to dryland wheat would help to minimize the decrease in residue inputs,

but most of the wheat biomass was produced aboveground, and the average root production of wheat was even lower than the root production of the dryland maize. Thus, even though wheat seems a viable option to maintain C inputs after the transition to dryland systems, reduced allocation to roots will likely limit the proportion of new C that is converted into SOC.

In addition to the importance of crop residues as C inputs, soil cover is important for water dynamics and protection from soil erosion (García-Prézac *et al* 2004, Luo *et al* 2010, Stewart *et al* 2019). Across the three years, irrigated maize had more soil cover than the dryland treatment (92% versus 45% soil cover). This impacted the storage of water during the fallow periods; in fall 2017 both maize treatments ended the growing season with the same soil moisture but before planting in spring 2018 gravimetric water content was higher in the irrigated treatment. Dryland maize may increase wind erosion risks relative to irrigated maize as soil cover was lower, and the distribution of residues more heterogeneous, probably the result of the residue being blown by the wind. Planting density and soil cover were lower in the dryland treatment, which resulted in the ability to generate greater wind speeds across the surface compared to the irrigated treatment, where the higher density of anchored plant stalks generated resistance for the residue to be blown. The low residue accumulation and its rapid loss during fallow increased the proportion of bare soil and the associated risk of wind erosion, an issue of high importance in the Great Plains, particularly during the spring (Farahani *et al* 1998, Hansen *et al* 2012). Soil cover was very similar in the wheat treatments due to similarities in planting densities and overall biomass production and no differences were observed due to irrigation. Soil cover in dryland wheat tends to be higher than in dryland maize (Schnarr 2019) resulting in another advantage of wheat over maize during the transition from irrigated to dryland.

4.2. Soil microbial responses to irrigation retirement

Besides the major changes observed in water dynamics and crop production, the effect of irrigation retirement on soil microbial communities was less evident and mainly limited to the transition under maize. The low treatment effect on PLFA indicators is somewhat surprising given the big differences in soil moisture and plant production. Both soil moisture and plant productivity generally have a positive impact on microbial biomass (Fierer *et al* 2009, Pérez-Guzmán *et al* 2020, Flynn *et al* 2021) but other factors that were part of our experimental design can also affect it. Irrigated maize received on average 80% more nitrogen fertilizer than the dryland treatment, which may reduce microbial biomass (Liebig *et al* 2002, Jian *et al* 2016). Also, no-till management increases microbial biomass in the topsoil (Chen *et al* 2020, Nunes *et al* 2020) and the effect of reduced tillage may be more important than crop rotation (Balota *et al* 2003). We think that the slow response of microbial communities to irrigation retirement may be related to the relatively lower effect of irrigation on root production and the transition to no-till that occurred simultaneously to retirement in our experiment. The biggest effect of irrigation retirement was on aboveground biomass production, as previously discussed, so in the long-term bigger differences in soil microbial communities between treatments can be expected as the crop residue decomposes and is transferred into the soil. In addition, the use of no-till during the experiment likely contributed to the increases in PLFA biomass across all treatments during the experimental period. Supporting this idea, no-till systems favor fungal populations (Acosta-Martínez *et al* 2007), and the fungal biomarker 18:2 ω 6 also increased during the experimental period, though its abundance was very low.

During fallow periods nitrate accumulates in the soil increasing the pool of inorganic nitrogen (Lamb *et al* 1985, Smika 1990). At the beginning of the experiment, the fallow period in the wheat plots was longer than in the maize treatments, and that was reflected by higher nitrate contents under wheat in Fall 2017. During the last two seasons, dryland maize growth was highly limited by water, with very low biomass accumulation. This resulted in low plant nitrogen uptake and an accumulation of nitrate in this treatment despite lower N fertilizer additions to dryland plots. Nitrate accumulation can have negative environmental impacts due to potential leaching losses (Dinnes *et al* 2002, Gregorich *et al* 2015) and nitrous oxide emissions during denitrification (Mosier *et al* 2006, Robertson and Vitousek 2009). Although the low soil moisture in dryland maize probably prevented large losses due to denitrification (Firestone and Davidson 1989, Wrage *et al* 2001, Gregorich *et al* 2015), the accumulation of reactive nitrogen increases the risk of losses and environmental impacts (Schlesinger 2009). Moreover, the decrease in nitrate concentrations between the fall and the following spring sampling (figure 4) is an indication of probable nitrogen losses during the winter and early spring.

Coincident with the observed differences in soil moisture and biomass production, irrigation retirement decreased soil enzyme activity in maize but not in wheat. Enzyme activity has been reported to be positively correlated with crop biomass production (Acosta-Martínez *et al* 2011), microbial biomass carbon (Acosta-Martínez *et al* 2007, Jian *et al* 2016, Bhandari *et al* 2018), and soil moisture (Sardans *et al* 2008, Brockett *et al* 2012, Burns *et al* 2013). All these factors were affected by irrigation retirement and probably influenced the differences in enzyme activity found in Fall 2019, when irrigated maize had almost 50% more enzyme activity than the retired treatment (figure 6). The decrease in enzyme activity after irrigation retirement in maize may

indicate changes in biogeochemical cycling and a potential decrease in residue decomposition (Acosta-Martínez *et al* 2018, Schimel 2018). These differences in enzyme activity occurred despite the low treatment effects on microbial biomass and no differences on microbial community composition, supporting the use of enzymes as early indicators of biological changes (Bandick and Dick 1999, Acosta-Martínez *et al* 2011, Cotton *et al* 2013). However, enzyme assays reflect the potential and not necessarily the realized *in situ* activity that can also be affected by changes in soil environmental conditions (Alster *et al* 2013, Schimel *et al* 2017). For example, reduced water availability may increase enzyme immobilization and reduce diffusion rates, decreasing enzyme efficiency and affecting litter decomposition independently of changes in potential enzyme activity (Alster *et al* 2013).

Although enzyme activity is assumed to increase with soil moisture (Sardans *et al* 2008, Brockett *et al* 2012, Steinweg *et al* 2012, Burns *et al* 2013), the response is not consistent as individual enzymes may have positive, null, or negative correlation with soil moisture (Sardans *et al* 2008, Bell *et al* 2009) and variable responses to drought or irrigation treatments (Sardans and Peñuelas 2005, Steinweg *et al* 2012, Alster *et al* 2013, Cotton *et al* 2013). In this study, all enzyme activities were positively correlated with gravimetric water content and air-drying the soil samples decreased the estimated irrigation effect, supporting a direct effect of soil moisture on potential microbial activity. It is usually recommended to conduct enzyme assays using fresh samples (German *et al* 2011, Burns *et al* 2013) but the use of air-dried samples to evaluate management practices is also common (Dick 2011, Cotton *et al* 2013, Acosta-Martínez *et al* 2018, Brennan and Acosta-Martínez 2019). The decrease in enzyme activity that we observed after air-drying the samples coincides with previous findings (Bandick and Dick 1999, Turner and Romero 2010, Wallenius *et al* 2010) although increased and unchanged activities have also been reported (Lorenz and Dick 2011, and references therein; Rao *et al* 2003). While some authors have found that sample handling did not impact conclusions (Bandick and Dick 1999), and others detected treatment effects in air-dried samples (Acosta-Martínez *et al* 2011, Cotton *et al* 2013, Pérez-Guzmán *et al* 2020) we found that air-drying the samples decreased the estimated irrigation effect on enzyme activity. After air-drying soil samples, enzyme activity is supposed to be stable (Lorenz and Dick 2011) and the estimated activity did not vary due to storage time for a year (Rao *et al* 2003). However, samples collected at higher moisture levels would take longer to reach stability when air-drying than samples with lower initial soil moisture. The higher relative decrease in enzyme activity during air-drying samples from the irrigated treatments may be related to the potential for enzyme degradation during the drying process. When the goal is to compare management practices that influence soil moisture, our results warn against the use of air-dried samples for the estimation of extracellular enzyme activity.

We also found a crop effect on enzyme activity that was consistent in both fresh and air-dried samples, suggesting that enzymes did not only respond to soil moisture. Higher enzyme activity in wheat than in dryland maize was expected, given the differences in biomass production and soil moisture. But the differences observed between wheat and irrigated maize cannot be explained by these factors. Litter addition stimulates enzyme activity (Dornbush 2007, Tian and Shi 2014), and the litter effect can be more important than the presence of growing plants (Dornbush 2007). Given the differences in the growing season of each crop, the time between crop harvest and soil sampling varied. In Fall 2019, we sampled the soil 99 d after wheat harvest but only 22 d after the harvest of irrigated maize. The warm conditions (average temperature 14 °C) and moisture availability (32 mm accumulated precipitation) during this longer fallow time before soil sampling in wheat likely stimulated initial stages of wheat litter decomposition and enzyme activity. Non-structural plant components and nitrogen are lost at a high rate during initial stages of litter decomposition (Cotrufo *et al* 2015). Although we did not observe statistical differences in the pool of dissolved organic nutrients, DON concentration in the last sampling was almost 30% higher in dryland wheat than in irrigated maize (9.70 versus 7.52 $\mu\text{g DON g soil}^{-1}$, figure 4). This coincided with a higher activity of L-leucine aminopeptidase and tyrosine aminopeptidase, involved in the hydrolysis of amino acid residues (Koch *et al* 2007, Cenini *et al* 2016), which supports the idea that enzyme activity was stimulated by the wheat residue decomposition processes.

The effects of irrigation on crop productivity and soil microbial properties and their evolution during irrigation retirement will be affected by edapho-climatic and management variables (Ghimire *et al* 2014, Calderón *et al* 2016, Cano *et al* 2018, Kukul and Irmak 2019). The adoption of conservation practices such as no till, crop intensification and diversification, or rotation with pastures, will have positive effects on soil health (Balota *et al* 2003, Acosta-Martínez *et al* 2004, Davis *et al* 2012, Cotton *et al* 2013, Rosenzweig *et al* 2018) and can help to minimize the negative impacts of irrigation retirement. In addition, producers may adopt alternative strategies to manage decreasing water supplies, including the adoption of more efficient irrigation technologies (Murley *et al* 2018, Oker *et al* 2020), deficit irrigation (Rudnick *et al* 2019), or the transition to crop rotations with lower water demands (Araya *et al* 2017, Schlegel *et al* 2017). These management decisions would also affect crop yields, economic profitability, and soil microbial communities (Araya *et al* 2017, Manning *et al* 2018, Flynn *et al* 2021). Our study was designed to isolate crop type and irrigation retirement effects on soil dynamics. Because of this, we decided to simplify the system and keep each treatment under a continuous single crop managed either

with or without irrigation, but we acknowledge that other management practices should be considered to mitigate crop yields and soil quality losses during future scenarios of declining water reserves.

5. Conclusions

It has been estimated that 24% of currently irrigated lands in the Ogallala Aquifer will be unable to support irrigated agriculture by 2100 (Deines *et al* 2020), and many farmers will have to stop irrigating and transition to dryland systems. While the transition to dryland is expected to reduce overall system productivity, little is known about the impact of irrigation retirement on soil microbial communities and SOC dynamics. After three years, we found that irrigation retirement had a stronger effect on a continuous maize agroecosystem compared to winter wheat cropping systems. Soil microbial communities were less affected by irrigation retirement than the evaluated crops. The high decrease in maize productivity and soil moisture had a negative impact on microbial activity but the effect on microbial community size was inconsistent and we did not find any evidence of changes in microbial community composition.

The comparison between irrigated maize and dryland wheat demonstrated that wheat is a better crop option to alleviate the negative impacts of irrigation retirement on crop production and soil microorganisms. Winter wheat productivity was less affected by irrigation retirement than continuous maize, which was expected due to the known adaptation of this crop to the climate of the OAR and lower irrigation requirements of wheat relative to irrigated maize. We found almost no differences in soil microbial dynamics in the retired treatment compared to the irrigated control after two wheat seasons with no-till management. However, there will be an inevitable decline in productivity after irrigation retirement, and the switch from maize to wheat would impact the proportion of carbon inputs belowground because root production was lower in wheat than in maize. This change in biomass allocation patterns may impact SOC formation and decrease the proportion of carbon from crop residues that remain in the system. Longer-term evaluations of SOC turnover and stocks evolution are necessary to fully assess the potential of different dryland crops and cropping systems to minimize the negative impacts of irrigation retirement on soil health.

Acknowledgments

We thank Karl Whitman, Mark Collins, and J R Herman for their support in the management of the experimental plots; Angie Moore, Dylan Casey, and several Student Research Assistants at the CSU Agroecology lab for help with sample processing; Cynthia Kallenbach for expert guidance on the enzyme protocol; Ann Hess for statistical advice; and Francesca Cotrufo for helpful comments on an early version of this manuscript. This work was supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, under award number 2016-68007-25066, 'Sustaining agriculture through adaptive management to preserve the Ogallala aquifer under a changing climate.', and by a Fulbright scholarship for graduate studies to Agustín Núñez.

Data availability statement

The data that support the findings of this study will be openly available following an embargo at the following URL/DOI: <http://ogallalawater.colostate.edu/OWCAP/>. Data will be available from 15 March 2023.

ORCID iDs

Agustín Núñez  <https://orcid.org/0000-0003-0558-1679>

Meagan Schipanski  <https://orcid.org/0000-0002-1661-9858>

References

- Abbate P E, Andrade F H and Culot J P 1995 The effects of radiation and nitrogen on number of grains in wheat *J. Agric. Sci.* **124** 351–60
- Acosta-Martínez V, Cano A and Johnson J 2018 Simultaneous determination of multiple soil enzyme activities for soil health-biogeochemical indices *Appl. Soil Ecol.* **126** 121–8
- Acosta-Martínez V, Lascano R, Calderón F, Booker J D, Zobeck T M and Upchurch D R 2011 Dryland cropping systems influence the microbial biomass and enzyme activities in a semiarid sandy soil *Biol. Fertil. Soils* **47** 655–67
- Acosta-Martínez V, Mikha M M and Vigil M F 2007 Microbial communities and enzyme activities in soils under alternative crop rotations compared to wheat—fallow for the Central Great Plains *Appl. Soil Ecol.* **37** 41–52
- Acosta-Martínez V, Zobeck T M and Allen V 2004 Soil microbial, chemical and physical properties in continuous cotton and integrated crop—livestock systems *Soil Sci. Soc. Am. J.* **68** 1875–84

- Alster C J, German D P, Lu Y and Allison S D 2013 Microbial enzymatic responses to drought and to nitrogen addition in a southern California grassland *Soil Biol. Biochem.* **64** 68–79
- Andales A A, Bauder T A and Arabi M 2014 A mobile irrigation water management system using a collaborative GIS and weather station networks *Practical Applications of Agricultural System Models to Optimize the Use of Limited Water*. ed L R Ahuja, L Ma and L Lascano (Madison, WI: ASA-CSSA-SSA) 53–84
- Araya A, Gowda P H, Golden B, Foster A J, Aguilar J, Currie R, Ciampitti I A and Prasad P V V 2019 Economic value and water productivity of major irrigated crops in the Ogallala aquifer region *Agric. Water Manag.* **214** 55–63
- Araya A, Kisekka I, Gowda P H and Prasad P V V 2017 Evaluation of water-limited cropping systems in a semi-arid climate using DSSAT-CSM *Agric. Syst.* **150** 86–98
- Balota E L, Colozzi-Filho A, Andrade D S and Dick R P 2003 Microbial biomass in soils under different tillage and crop rotation systems *Biol. Fertil. Soils* **38** 15–20
- Bandick A K and Dick R P 1999 Field management effects on soil enzyme activities *Soil Biol. Biochem.* **31** 1471–9
- Bates D, Mächler M, Bolker B M and Walker S C 2015 Fitting linear mixed-effects models using lme4 *J. Stat. Softw.* **67** 1–48
- Bell C W, Acosta-Martínez V, McIntyre N E, Cox S, Tissue D T and Zak J C 2009 Linking microbial community structure and function to seasonal differences in soil moisture and temperature in a chihuahuan desert grassland *Soil Microbiol.* **58** 827–42
- Bhandari K B, West C P, Acosta-Martínez V, Cotton J and Cano A 2018 Soil health indicators as affected by diverse forage species and mixtures in semi-arid pastures *Appl. Soil Ecol.* **132** 179–86
- Bhatta M, Eskridge K M, Rose D J, Santra D K, Baenziger P S and Regassa T 2017 Seeding rate, genotype, and topdressed nitrogen effects on yield and agronomic characteristics of winter wheat *Crop Sci.* **57** 951–63
- Bradford M A, Wieder W R, Bonan G B, Fierer N, Raymond P A and Crowther T W 2016 Managing uncertainty in soil carbon feedbacks to climate change *Nat. Clim. Chang.* **6** 751–8
- Brennan E B and Acosta-Martínez V 2019 Cover crops and compost influence soil enzymes during six years of tillage-intensive, organic vegetable production *Soil Sci. Soc. Am. J.* **83** 624–37
- Brockett B F T, Prescott C E and Grayston S J 2012 Soil moisture is the major factor influencing microbial community structure and enzyme activities across seven biogeoclimatic zones in western Canada *Soil Biol. Biochem.* **44** 9–20
- Burns R G, DeForest J L, Marxsen J, Sinsabaugh R L, Stromberger M E, Wallenstein M D, Weintraub M N and Zoppini A 2013 Soil enzymes in a changing environment: Current knowledge and future directions *Soil Biol. Biochem.* **58** 216–34
- Calderón F J, Nielsen D C, Acosta-Martínez V, Vigil M F and Lyon D 2016 Cover crop and irrigation effects on soil microbial communities and enzymes in semiarid agroecosystems of the central great plains of North America *Pedosphere* **26** 192–205
- Canarini A, Carrillo Y, Mariotte P, Ingram L and Dijkstra F A 2016 Soil microbial community resistance to drought and links to C stabilization in an Australian grassland *Soil Biol. Biochem.* **103** 171–80
- Cano A, Núñez A, Acosta-Martínez V, Schipanski M E, Ghimire R, Rice C and West C 2018 Current knowledge and future research directions to link soil health and water conservation in the Ogallala Aquifer region *Geoderma* **328** 109–18
- Cenini V L, Fornara D A, McMullan G, Ternan N, Carolan R, Crawley M J, Clément J and Lavorel S 2016 Linkages between extracellular enzyme activities and the carbon and nitrogen content of grassland soils *Soil Biol. Biochem.* **96** 198–206
- Chen H, Dai Z, Veach A M, Zheng J, Xu J and Schadt C W 2020 Global meta-analyses show that conservation tillage practices promote soil fungal and bacterial biomass *Agric. Ecosyst. Environ.* **293** 106841
- Ciampitti I A and Vyn T J 2012 Physiological perspectives of changes over time in maize yield dependency on nitrogen uptake and associated nitrogen efficiencies: a review *F. Crop. Res.* **133** 48–67
- Conant R T, Dalla-betta P, Klopatek C C and Klopatek J M 2004 Controls on soil respiration in semiarid soils *Soil Biol. Biochem.* **36** 945–51
- Cotrufo M F, Soong J L, Horton A J, Campbell E E, Haddix M L, Wall D H and Parton W J 2015 Formation of soil organic matter via biochemical and physical pathways of litter mass loss *Nat. Geosci.* **8** 776–9
- Cotton J, Acosta-Martínez V, Moore-Kucera J and Burow G 2013 Early changes due to sorghum biofuel cropping systems in soil microbial communities and metabolic functioning *Biol. Fertil. Soils* **49** 403–13
- Davis A S, Hill J D, Chase C A, Johanns A M and Liebman M 2012 Increasing cropping system diversity balances productivity, profitability and environmental health *PLoS One* **7** 1–8
- Davis K F, Rosa L, Passera C, Chiarelli D D, D'Odorico P and Rulli M C 2018 Closing the yield gap while ensuring water sustainability *Environ. Res. Lett.* **13** 104002
- Deines J M, Schipanski M E, Golden B, Zipper S C, Nozari S, Rottler C, Guerrero B and Sharda V 2020 Transitions from irrigated to dryland agriculture in the Ogallala Aquifer: land use suitability and regional economic impacts *Agric. Water Manag.* **233** 106061
- Denef K, Stewart C E, Brenner J and Paustian K 2008 Does long-term center-pivot irrigation increase soil carbon stocks in semi-arid agroecosystems? *Geoderma* **145** 121–9
- Dick W A 2011 Development of a soil enzyme reaction assay *Methods of Soil Enzymology*. 9 (Madison, Wisconsin, USA: Soil Science Society of America) 71–84
- Dinnes D L, Karlen D L, Jaynes D B, Kaspar T C, Hatfield J L, Colvin T S and Cambardella C A 2002 Nitrogen management strategies to reduce nitrate leaching in tile-drained midwestern soils *Agron. J.* **94** 153–71
- Doane T A and Horwath W R 2003 Spectrophotometric determination of nitrate with a single reagent *Anal. Lett.* **36** 2713–22
- Dornbush M E 2007 Grasses, litter, and their interaction affect microbial biomass and soil enzyme activity *Soil Biol. Biochem.* **39** 2241–9
- FAO 2001 *Food Balance Sheets: A Handbook* (Rome: Food and Agriculture Organization of the United Nations) (<http://www.fao.org/3/a-x9892e.pdf>)
- FAO 2011 *The State of the World's Land and Water Resources for Food and Agriculture (SOLAW) - Managing Systems at Risk*. (Rome and Earthscan, London: Food and Agriculture Organization of the United Nations) (<https://fao.org/3/i1688e/i1688e00.htm>)
- Farahani H J, Peterson G A and Westfall D G 1998 Dryland cropping intensification: a fundamental solution to efficient use of precipitation *Adv. Agron.* **64** 197–223
- Fierer N, Strickland M S, Liptzin D, Bradford M A and Cleveland C C 2009 Global patterns in belowground communities *Ecol. Lett.* **12** 1238–49
- Fierer N, Wood S A and Bueno de Mesquita C P 2021 How microbes can, and cannot, be used to assess soil health *Soil Biol. Biochem.* **153** 108111
- Firestone M K and Davidson E A 1989 Microbiological basis of NO and N₂O production and consumption in soil *Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere: report of the Dahlem workshop on exchange of trace gases between terrestrial ecosystems and the atmosphere* (47) 47 (New York, NY: Wiley) 7–21
- Fischer R A 1985 Number of kernels in wheat crops and the influence of solar radiation and temperature *J. Agric. Sci.* **105** 447–61

- Flynn N E, Comas L H, Stewart C E and Fonte S J 2021 Deficit irrigation drives maize root distribution and soil microbial communities with implications for soil carbon dynamics *Soil Sci. Soc. Am. J.* **85** 412–22
- Fox J and Weisberg S 2011 Multivariate linear models in R *An R Companion to Applied Regression*. (Los Angeles: Thousand Oaks)
- Franzluebbers A J, Hons F M and Zuberer D A 1994 Long-term changes in soil carbon and nitrogen pools in wheat management systems *Soil Sci. Soc. Am. J.* **58** 1639–45
- Frostegård Å and Bååth E 1996 The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil *Biol. Fertil. Soils* **22** 59–65
- Frostegård Å, Bååth E and Tunlid A 1993 Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipid fatty acid analysis *Soil Biol. Biochem.* **25** 723–30
- Fuchslueger L, Bahn M, Fritz K, Hasibeder R and Richter A 2014 Experimental drought reduces the transfer of recently fixed plant carbon to soil microbes and alters the bacterial community composition in a mountain meadow *New Phytol.* **201** 916–27
- Fulton-Smith S and Cotrufo M F 2019 Pathways of soil organic matter formation from above and belowground inputs in a Sorghum bicolor bioenergy crop *GCB Bioenergy* **11** 971–87
- García Suárez F, Fulginiti L E and Perrin R K 2018 What is the use value of irrigation water from the high plains aquifer? *Am. J. Agric. Econ.* **0** 1–12
- García-Préchac F, Ernst O R, Siri Prieto G and Terra J 2004 Integrating no-till into crop-pasture rotations in Uruguay *Soil Tillage Res.* **77** 1–13
- German D P, Weintraub M N, Grandy A S, Lauber C L, Rinkes Z L and Allison S D 2011 Optimization of hydrolytic and oxidative enzyme methods for ecosystem studies *Soil Biol. Biochem.* **43** 1387–97
- Ghimire R, Norton J B, Stahl P D and Norton U 2014 Soil microbial substrate properties and microbial community responses under irrigated organic and reduced-tillage crop and forage production systems *PLoS One* **9** e103901
- Gregorich E, Janzen H H, Helgason B and Ellert B H 2015 Nitrogenous gas emissions from soils and greenhouse gas effects *Adv. Agric.* **132** 39–74
- Halvorson A D and Schlegel A J 2012 Crop rotation effect on soil carbon and nitrogen stocks under limited irrigation *Agron. J.* **104** 1265–73
- Halvorson A D and Stewart C E 2015 Stover removal affects no-till irrigated corn yields, soil carbon, and nitrogen *Agron. J.* **107** 1504–12
- Hamel C, Hanson K, Selles F, Cruz A F, Lemke R, McConkey B and Zentner R 2006 Seasonal and long-term resource-related variations in soil microbial communities in wheat-based rotations of the Canadian prairie *Soil Biol. Biochem.* **38** 2104–16
- Hansen N C, Allen B L, Baumhardt R L and Lyon D J 2012 Research achievements and adoption of no-till, dryland cropping in the semi-arid U.S. Great Plains *F. Crop. Res.* **132** 196–203
- Hornbeck R and Keskin P 2014 The historically evolving impact of the Ogallala Aquifer : agricultural adaptation to groundwater and drought *Am. Econ. J. Appl. Econ.* **6** 190–219
- Jian S, Li J, Chen J, Wang G, Mayes M A, Dzantor K E, Hui D and Luo Y 2016 Soil extracellular enzyme activities, soil carbon and nitrogen storage under nitrogen fertilization : a meta-analysis *Soil Biol. Biochem.* **101** 32–43
- Kallenbach C, Frey S D and Grandy A S 2016 Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls *Nat. Commun.* **7** 13630
- Kane D A, Bradford M A, Fuller E, Oldfield E E and Wood S A 2021 Soil organic matter protects US maize yields and lowers crop insurance payouts under drought *Environ. Res. Lett.* **16** 044018
- Koch O, Tschirko D and Kandeler E 2007 Temperature sensitivity of microbial respiration, nitrogen mineralization, and potential soil enzyme activities in organic alpine soils *Global Biogeochem. Cycles* **21** 1–11
- Kukul M S and Irmak S 2019 Irrigation-limited yield gaps: trends and variability in the united states post-1950 *Environ. Res. Commun.* **1** 061005
- Kuznetsova A, Brockhoff P B and Christensen R H B 2017 lmerTest package: tests in linear mixed effects models *J. Stat. Softw.* **82** 1–26
- Laflen J M, Amemiya M and Hintz E A 1981 Measuring crop residue cover *J. Soil Water Conserv.* **36** 341–3 (<https://www.jswconline.org/content/36/6/341>)
- Lamb J A, Peterson G A and Fenster C R 1985 Fallow nitrate accumulation in a wheat-fallow rotation as affected by tillage system *Soil Sci. Soc. Am. J.* **49** 1441–6
- Lamm F R, Stone L R and Brien D M O 2007 Crop production and economics in Northwest Kansas as related to irrigation capacity *Appl. Eng. Agric.* **23** 737–46
- Lehmann J, Bossio D A, Kögel-Knabner I and Rillig M C 2020 The concept and future prospects of soil health *Nat. Rev. Earth Environ.* **1** 544–553
- Lenth R, Singmann H, Love J, Buerkner P and Herve M 2018 Emmmeans: estimated marginal means, aka least-squares means *R Package. Version 1.3*
- Liebig M A, Varvel G E, Doran J W and Wienhold B J 2002 Crop sequence and nitrogen fertilization effects on soil properties in the Western Corn Belt *Soil Sci. Soc. Am. J.* **66** 596–601
- Lorenz N and Dick R P 2011 Sampling and pretreatment of soil before enzyme analysis *Methods of Soil Enzymology*. (SSSA Book Series 9) 9 (Madison, Wisconsin, USA: Soil Science Society of America) 85–101
- Luo Z, Wang E and Sun O J 2010 Can no-tillage stimulate carbon sequestration in agricultural soils? A meta-analysis of paired experiments *Agric. Ecosyst. Environ.* **139** 224–31
- Ma L, Guo C, Lü X, Yuan S and Wang R 2015 Soil moisture and land use are major determinants of soil microbial community composition and biomass at a regional scale in northeastern China *Biogeosciences* **12** 2585–96
- Manning D T, Lurbé S, Comas L H, Trout T J, Flynn N E and Fonte S J 2018 Economic viability of deficit irrigation in the Western US *Agric. Water Manag.* **196** 114–23
- Manzoni S, Schimel J P and Porporato A 2012 Responses of soil microbial communities to water stress: results from a meta-analysis *Ecology* **93** 930–8
- Mazzilli S R, Kemanian A R, Ernst O R, Jackson R B and Piñeiro G 2015 Greater humification of belowground than aboveground biomass carbon into particulate soil organic matter in no-till corn and soybean crops *Soil Biol. Biochem.* **85** 22–30
- Mosier A R, Halvorson A D, Reule C A and Liu X J 2006 Net global warming potential and greenhouse gas intensity in irrigated cropping systems in Northeastern Colorado *J. Environ. Qual.* **35** 1584–98
- Murley C B, Sharma S, Warren J G, Arnall D B and Raun W R 2018 Yield response of corn and grain sorghum to row offsets on subsurface drip laterals *Agric. Water Manag.* **208** 357–62
- Ndiaye E L, Sandeno J M, McGrath D and Dick R P 2000 Integrative biological indicators for detecting change in soil quality *Am. J. Altern. Agric.* **15** 26–36
- Norwood C A 2000 Water use and yield of limited-irrigated and dryland corn *Soil Sci. Soc. Am. J.* **64** 365–70

- Nunes M R, Karlen D L, Veum K S, Moorman T B and Cambardella C A 2020 Biological soil health indicators respond to tillage intensity: a US meta-analysis *Geoderma* **369** 114335
- Oker T E, Kisekka I, Sheshukov A Y, Aguilar J and Rogers D 2020 Evaluation of dynamic uniformity and application efficiency of mobile drip irrigation *Irrig. Sci.* **38** 17–35
- Oksanen J et al 2013 Vegan: Community Ecology Package *R Package Version 2* 1–88
- Oldfield E E, Bradford M A and Wood S A 2019 Global meta-analysis of the relationship between soil organic matter and crop yields *SOIL* **5** 15–32
- Otegui M E, Andrade F H and Suero E E 1995 Growth, water use, and kernel abortion of maize subjected to drought at silking *F. Crop. Res.* **40** 87–94
- Pérez-Guzmán L, Acosta-Martínez V, Phillips L A and Mauget S A 2020 Resilience of the microbial communities of semiarid agricultural soils during natural climatic variability events *Appl. Soil Ecol.* **149** 103487
- R Core Team 2020 R: A language and environment for statistical computing
- Rao M A, Sannno F, Nocerino G, Puglisi E and Gianfreda L 2003 Effect of air-drying treatment on enzymatic activities of soils affected by anthropogenic activities *Biol. Fertil. Soils* **38** 327–32
- Rasse D P, Rumpel C and Dignac M-F 2005 Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation *Plant Soil* **269** 341–56
- Rawls W J, Pachepsky Y A, Ritchie J C, Sobecki T M and Bloodworth H 2003 Effect of soil organic carbon on soil water retention *Geoderma* **116** 61–76
- Ren C, Zhao F, Shi Z, Chen J, Han X, Yang G, Feng Y and Ren G 2017 Differential responses of soil microbial biomass and carbon-degrading enzyme activities to altered precipitation *Soil Biol. Biochem.* **115** 1–10
- Richey A S, Thomas B F, Lo M-H, Reager J T, Famiglietti J S, Voss K, Swenson S and Rodell M 2015 Quantifying renewable groundwater stress with GRACE *Water Resour. Res.* **51** 5217–38
- Robertson G P and Vitousek P M 2009 Nitrogen in agriculture: balancing the cost of an essential resource *Annu. Rev. Environ. Resour.* **34** 97–125
- Rosenzweig S T, Fonte S J and Schipanski M E 2018 Intensifying rotations increases soil carbon, fungi, and aggregation in semi-arid agroecosystems *Agric. Ecosyst. Environ.* **258** 14–22
- Rosenzweig S T and Schipanski M E 2019 Landscape-scale cropping changes in the high plains: economic and environmental implications *Environ. Res. Lett.* **14** 124088
- Rudnick D R et al 2019 Deficit irrigation management of maize in the high plains aquifer region: a review *JAWRA J. Am. Water Resour. Assoc.* **55** 38–55
- Saiya-Cork K R, Sinsabaugh R L and Zak D R 2002 The effects of long term nitrogen deposition on extracellular enzyme activity in an Acer saccharum forest soil *Soil Biol. Biochem.* **34** 1309–15
- Sardans J and Peñuelas J 2005 Drought decreases soil enzyme activity in a Mediterranean Quercus ilex L. forest *Soil Biol. Biochem.* **37** 455–61
- Sardans J, Peñuelas J and Estiarte M 2008 Changes in soil enzymes related to C and N cycle and in soil C and N content under prolonged warming and drought in a Mediterranean shrubland *Appl. Soil Ecol.* **39** 223–35
- Schaeffer S M, Homyak P M, Boot C M, Roux-Michollet D and Schimel J P 2017 Soil carbon and nitrogen dynamics throughout the summer drought in a California annual grassland *Soil Biol. Biochem.* **115** 54–62
- Schimel J P 2018 Life in dry soils: effects of drought on soil microbial communities and processes *Annu. Rev. Ecol. Evol. Syst.* **49** 409–32
- Schimel J P, Becerra C A and Blankinship J 2017 Estimating decay dynamics for enzyme activities in soils from different ecosystems *Soil Biol. Biochem.* **114** 5–11
- Schlegel A J, Assefa Y, Haag L A, Thompson C R, Holman J D and Stone L R 2017 Yield and soil water in three dryland wheat and grain sorghum rotations *Agron. J.* **109** 227–38
- Schlesinger W H 2009 On the fate of anthropogenic nitrogen *Proc. Natl Acad. Sci.* **106** 203–8
- Schnarr C 2019 *Crop Residue: A Hero's Journey from Biomass to Soil Carbon in Eastern Colorado Dryland Crop Rotation Systems* Colorado State University (<https://hdl.handle.net/10217/195370>)
- Service, UNAS 2017 NASS - Quick Stats. (USDA National Agricultural Statistics Service) [WWW Document]. URL (<https://data.nal.usda.gov/dataset/nass-quick-stats>). (accessed 2.25.21)
- Sherrod L A, Ahuja L R, Hansen N C, Ascough J C, Westfall D G and Peterson G A 2014 Soil and rainfall factors influencing yields of a dryland cropping system in Colorado *Agron. J.* **106** 1179–92
- Sims G K, Ellsworth T R and Mulvaney R L 1995 Microscale determination of inorganic nitrogen in water and soil extracts *Commun. Soil Sci. Plant Anal.* **26** 303–16
- Smidt S J, Haacker E M K, Kendall A D, Deines J M, Pei L, Cotterman K A, Li H, Liu X, Basso B and Hyndman D W 2016 Complex water management in modern agriculture: trends in the water-energy-food nexus over the High Plains Aquifer *Sci. Total Environ.* **566–567** 988–1001
- Smika D E 1990 Fallow management practices for wheat production in the central great plains *Agron. J.* **82** 319–23
- Smith P 2004 How long before a change in soil organic carbon can be detected? *Glob. Chang. Biol.* **410** 1878–83
- Steinweg J M, Dukes J S and Wallenstein M D 2012 Modeling the effects of temperature and moisture on soil enzyme activity: linking laboratory assays to continuous field data *Soil Biol. Biochem.* **55** 85–92
- Stewart C E, Roosendaal D L, Sindelar A, Pruessner E, Jin V L and Schmer M R 2019 Does no-tillage mitigate stover removal in irrigated continuous corn? A multi-location assessment *Soil Sci. Soc. Am. J.* **83** 733–42
- Tian L and Shi W 2014 Short-term effects of plant litter on the dynamics, amount, and stoichiometry of soil enzyme activity in agroecosystems *Eur. J. Soil Biol.* **65** 23–9
- Turner B L and Romero T E 2010 Stability of hydrolytic enzyme activity and microbial phosphorus during storage of tropical rain forest soils *Soil Biol. Biochem.* **42** 459–65
- U.S. Department of Agriculture, NRCS 2019 *Soil Survey Geographic (SSURGO) database for Larimer County Area* (Colorado) [WWW Document]. URL (<https://websoilsurvey.sc.egov.usda.gov/>) (accessed 3.27.20)
- Wade J, Culman S W, Logan J A R, Poffenbarger H, Demyan M S, Grove J H, Mallarino A P, McGrath J M, Ruark M and West J R 2020 Improved soil biological health increases corn grain yield in N fertilized systems across the Corn Belt *Sci Rep.* **10** 1–9
- Wallenius K, Rita H, Simpanen S, Mikkonen A and Niemi R M 2010 Sample storage for soil enzyme activity and bacterial community profiles *J. Microbiol. Methods* **81** 48–55
- Whittemore D O, Butler J J and Wilson B B 2016 Assessing the major drivers of water-level declines: new insights into the future of heavily stressed aquifers *Hydrol. Sci. J.* **61** 134–45
- Wrage N, Velthof G, van Beusichem M and Oenema O 2001 Role of nitrifier denitrification in the production of nitrous oxide *Soil Biol. Biochem.* **33** 1723–32

- Zelles L 1999 Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review *Biol. Fertil. Soils* **111**–29
- Zhou G, Zhou X, Nie Y, Bai S H, Zhou L, Shao J, Cheng W, Wang J, Hu F and Fu Y 2018 Drought-induced changes in root biomass largely result from altered root morphological traits: evidence from a synthesis of global field trials *Plant Cell Environ.* **41** 2589–99
- Schnarr C 2019 *Crop Residue: A Hero's Journey from Biomass to Soil Carbon in Eastern Colorado Dryland Crop Rotation Systems* Colorado State University (<https://hdl.handle.net/10217/195370>)